

r3

DISTRIBUTION PATTERNS OF COMMON SEASTARS OF THE MIDDLE ATLANTIC CONTINENTAL SHELF OF THE NORTHWEST ATLANTIC (GULF OF MAINE TO CAPE HATTERAS)

D. R. FRANZ, E. K. WORLEY, AND A. S. MERRILL¹

Biology Department, Brooklyn College, CUNY, Brooklyn, N. Y. 11210

ABSTRACT

Twenty-five asteroid species were collected during four groundfish surveys carried out by the National Marine Fisheries Service on the continental shelf from the Gulf of Maine to Cape Hatteras. Six species groups were identified, based on similarities in geographic ranges, bottom-temperature relationships, and depth distributions.

Species endemic to the boreal Northwest Atlantic include a group of middle- to outer-shelf species usually found in deeper waters north of Cape Hatteras, and a group of species with broad depth ranges whose inshore depth limits decrease from north to south (the phenomenon of submergence).

Seastars found only in the Gulf of Maine in this survey include a group of subarctic species (which do not live in arctic waters), and a group of arctic-subarctic species (which may live in arctic waters). The latter are wider-ranging, occurring throughout the Arctic Ocean and into the North Pacific. Seasonally variable bottom isotherms associated with Georges Bank restrict the geographical distribution of the boreal and arctic-subarctic faunal groups of seastars.

Speculations are presented concerning when and where these groups originated. The possible effects of competition between *Asterias forbesi* and *A. vulgaris* on their distribution patterns are discussed.

INTRODUCTION

The general distribution patterns of the seastars of the Middle Atlantic continental shelf of eastern North America were established by A. E. Verrill (1878, 1894, 1895). H. L. Clark (1904) and W. R. Coe (1912) provided additional information on the echinoderms of southern New England. More recently, Gray *et al.* (1968) published a detailed account of the distributions of seastars of the North Carolina continental shelf, and Grainger (1964, 1966) contributed a definitive study of the seastars of Canadian arctic and subarctic coastal waters. The present report documents the distribution patterns of asteroids on the middle Atlantic continental shelf from the Gulf of Maine to Cape Hatteras, North Carolina, and provides further information on the general distribution patterns of common seastars.

This investigation also sought distribution patterns based on extended geographical ranges, depth distributions, and correlations with bottom temperatures. Such patterns identify groups of species with similar latitudinal and depth distributions. In this paper and elsewhere (Franz and Merrill, 1980a, b) we propose that these groups may be explained in terms of common origins in space and time. We

Received 19 January 1981; accepted 20 March 1981.

¹ National Marine Fisheries Service, Woods Hole, MA 02543

hope eventually to compare the distribution patterns of asteroids with those of other invertebrate taxa (*e.g.* Mollusca) that are represented adequately in the fossil record, to test hypotheses on the origins of faunal groups.

We suggest that distribution patterns of groups of seastars in the Northwest Atlantic are determined primarily by temperature and (less importantly) by other environmental factors, but that the ultimate causes probably are paleobiogeographical. With some exceptions, seastars that live north of Cape Hatteras appear to be most closely related to the fauna of the North Pacific. Certain aspects of present distribution patterns may be related to the periods of transarctic migration, *i.e.* the amount of time species have had to become adapted to the Northwest Atlantic environment.

MATERIALS AND METHODS

Seastars were collected during four research cruises by personnel of the National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries): R/V Delaware Cruise 60-7, A Sea Scallop Survey, Block Island to Cape Hatteras, 11-21 May 1960; R/V Delaware II, Cruise 75-19, A Winter Groundfish Survey from Martha's Vineyard to Cape Hatteras, 1-18 December 1975; R/V Delaware II, Cruise 78-01, A Surf Clam Survey from Long Island to Cape Hatteras, 4 January to 11 February 1978; R/V Delaware II, Cruise 79-03; and R/V Albatross IV, Cruise 79-04, A Groundfish Survey from the Gulf of Maine to Cape Hatteras, 26 March to 26 May 1979.

Bottom samples were taken with a standard (3.05 m) sea scallop dredge on the 60-7 Cruise, and a hydraulic surf clam dredge with a 1.2 m (48 in.) knife on Cruise 78-01. On Cruises 75-19, 79-03, and 79-04, seastars were collected by standard otter trawls. All seastars were bagged and frozen immediately. Asteroids from Cruise 60-7 were identified by Dr. M. J. Cerame-Vivas (University of Puerto Rico). Other collections were sorted and identified by the authors and verified by M. E. Downey (United States National Museum of Natural History, where selected samples of these animals have been deposited).

For all of the species encountered in this study, we have indicated the bottom temperatures that most closely correspond with their geographical distributions. Average minimum bottom temperatures occur in February and average maximum temperatures in September. The bottom temperature data are from Colton and Stoddard (1973) for the continental shelf from Nova Scotia to New Jersey, and from Walford and Wickland (1968) for the area from Long Island to Cape Hatteras, North Carolina, supplemented by Bowman and Wunderlich (1977) for the New York Bight. These correlations do not demonstrate thermal limits decisively, although they do indicate an approximate range of critical temperatures that may determine distribution.

Biogeographical terminology

In describing the ranges of cold-water seastars, we use the terms arctic and subarctic as defined by Dunbar (1951). The arctic zone is characterized by bottom temperatures near freezing (-1.7°C) throughout the year. The subarctic zone is a region of mixed arctic and Atlantic water entirely free of sea ice in the summer, in which bottom temperatures are usually 2°C . In the North Atlantic, the subarctic zone extends from Newfoundland to the Barents Sea, including the Labrador and West Greenland continental shelves (Dunbar, 1953). Temperature-salinity dia-

grams for this area (Dunbar, 1951) show that at depths greater than 50 m, temperatures range seasonally from *ca.* 1° to 7°C. Bottom temperatures remain less than 7°C throughout the year in the Gulf of Maine (Colton and Stoddard, 1973) except near shore and in the southwestern region, where seasonal contrasts are somewhat greater. Thus, we include the major basins of the Gulf of Maine as part of the subarctic zone.

The boreal zone of the European North Atlantic was defined originally as the area of the continental shelf inhabited by the cold-temperate fauna of the Northern European coast (Ekman, 1953). A significant number of these species (the amphiatlantic fauna) have ranges which extend into the Northwest Atlantic. Here, the boreal zone is defined as that portion of the continental shelf delimited by the ranges of these amphiatlantic species *i.e.* Labrador to Cape Hatteras. Some boreal species have restricted ranges within these boundaries, and some may extend somewhat farther north. The boreal species discussed in this paper have ranges which include the continental shelf from the eastern tip of Georges Bank to Cape Hatteras, excluding the Gulf of Maine. Some species which have arctic or subarctic distributions follow cold isotherms south of latitude 42°N down the continental slope, but are not found on the shelf. These species are not considered to be in "boreal waters" as defined above.

Hall (1964), Sanders (1968, 1969), and others emphasized the differences in the marine climates of the two Atlantic boreal zones. Temperature fluctuations are more rapid and seasonally more extreme on the American continental shelf than in the Northeastern Atlantic. On Georges Bank, for example, bottom temperatures may range seasonally from 4°–16°C (Colton and Stoddard, 1973) as compared to 9°–17°C near the southwestern entrance to the English Channel (Ekman, 1953).

RESULTS

The 24 species included in this report are presented in the following categories: (1) subtropical-tropical continental shelf species; (2) Atlantic coast species ranging extensively both north and south of Cape Hatteras; (3) Northwest Atlantic outer-shelf boreal species; (4) Northwest Atlantic subarctic-boreal species; (5) subarctic species; (6) arctic-subarctic species.

Group 1: Subtropical-tropical continental shelf species (Table I)

Of the five subtropical-tropical species encountered in this study, only *Luidia clathrata* and *Astropecten articulatus* were collected on the inner and middle shelf near and north of Cape Hatteras (Figs. 1, 2). Both species were found in progressively deeper sites north of Cape Hatteras (Figs. 17, 18). The northward distributions of *A. articulatus* and *L. clathrata* roughly follow the average position of the 10°C winter bottom isotherm, but do not correlate with summer bottom temperatures north of Cape Hatteras (Figs. 3, 4). The northward submergence of these species may reflect warm bottom isotherms associated with the outer continental shelf north of Cape Hatteras, as Hazel (1970) suggested to explain patterns in benthic ostracods.

Stephanasterias gracilis (Figs. 2, 18) was found at four sites along the outer continental shelf northeast of Cape Hatteras over a depth range of 106–146 m (Cruise 60-7 only). This corresponds to the northward range limits reported by Gray *et al.* (1968). Single specimens of both *Narcissia trigonaria* (not mapped)

and *Luidia alternata* (not mapped) were collected at stations south of Cape Hatteras (Table I).

Group 2: Atlantic Coast species that range extensively both north and south of Cape Hatteras

Only one species in this survey, *Asterias forbesi*, ranges extensively both north and south of Cape Hatteras. It is found from Casco Bay, Maine (based on records in the United States National Museum) south to the Florida Keys, although it is evidently rare south of latitude 28°N (Downey, 1973).

In the zone from Cape Hatteras to Cape Cod (Fig. 5), *A. forbesi* was distributed over the entire continental shelf, except north of 40°N, where collections were largely confined to the inner shelf, on Nantucket Shoals, and in Cape Cod Bay (in agreement with Clark, 1904). Despite its distribution over much of the continental shelf, *A. forbesi* was collected most frequently at stations less than 30 m in depth (Fig. 21). The relationship between bottom temperatures and distribution is discussed below, in conjunction with *A. vulgaris*.

Group 3: Northwest Atlantic outer shelf boreal species (Table II)

The four species composing the Northwest Atlantic outer shelf boreal species, *Astropecten americanus*, *Sclerasterias tanneri*, *Porania insignis*, and *Odontaster hispidus*, are restricted to the middle and outer continental shelf (Georges Bank to Cape Hatteras) (Table II), at depths greater than 50 m (with the exception of *A. americanus*). Both *A. americanus* and *S. tanneri* exhibit northward submergence.

A. americanus is found only in areas of the continental shelf where winter bottom temperatures remain above 5°–6°C (Fig. 6). These isotherms cross the 100 m contour on the outer edge of Georges Bank, south of Nantucket. Winter temperatures on the inner shelf from Georges Bank to northern North Carolina generally remain below 7.5°C, probably accounting for the absence of *A. americanus*. Summer bottom temperatures coinciding with the geographical distribution of *A. americanus* range from about 10°C (off Georges Bank) to about 20°C on the outer shelf near Cape Hatteras.

The distribution of *A. americanus* may also be limited by warm summer temperatures above 20°C, possibly accounting for its absence from the inner continental shelf off northern North Carolina and from almost the entire shelf south of Cape Hatteras. Near to and south of Cape Hatteras, *A. americanus* is replaced by *A. articulatus*. Interactions between these species in relation to environmental factors, and especially to seasonal marine climate, should be investigated.

A. americanus (Fig. 19) is found in progressively deeper waters northward. Its upper depth limit declines gradually from about 25 m near Cape Hatteras to about 50 m at latitude 40°30'N, followed by a sharper decline northward to 149 m near its northern range limit on Georges Bank. As with *A. articulatus* and *Luidia clathrata*, this northward submergence implies the tracking of warmer winter isotherms into deeper waters.

The distribution of *Sclerasterias tanneri* (Figs. 7, 20) is qualitatively similar to *A. americanus* except that *S. tanneri* is more strictly confined to the outer continental shelf and to the upper slope. This species occurs where winter bottom

TABLE I

Subtropical/tropical species—present survey.

Species	Geographical range	Reference	Northern limit	Depth range (m)	Previously known depth range (m)
<i>Astropecten articulatus</i> (Say)	Off Chesapeake Bay to Columbia	Downey (1973)	36°23' 74°54'	18-44	18-165
<i>Luidia clathrata</i> (Say)	New Jersey* to Brazil	Downey (1973)	37°06' 74°48'	18-74	0-175
<i>Stephanasterias gracilis</i> Verrill	North Carolina to Lesser Antilles	Gray <i>et al.</i> (1968)	36°52' 74°36'	106-146	145-370
<i>Narcissia trigonaria</i> Sladen	North Carolina to Brazil	Downey (1973)	34°08' 76°12'	65	37-91
<i>Luidia alternata</i> (Say)	North Carolina to Brazil	Downey (1973)	34°02' 76°25'	40	10-200

* The New Jersey record may be in error

TABLE II

Outer shelf boreal species—present survey.

Species	Geographical range	Reference	Northern limit	Southern limit	Depth range (m)	Previously known depth range (m)
<i>Astropecten americanus</i> Verrill	40°23'N to 35°39'N	Verrill (1895)	42°53'N, 69°18'W	35°25'N, 75°13'W	26-168	55-542
<i>Sclerasterias tanneri</i> Verrill	40°81'N to 35°10'N	Verrill (1895)	42°09'N, 66°26'W	36°36'N, 74°52'W	62-186	88-355
<i>Odontaster hispidus</i> Verrill	Cape Cod to Florida	Gray <i>et al.</i> (1968)	39°44'N, 72°04'W	36°52'N, 74°36'W	146	30-875
<i>Porania insignis</i> Verrill	Georges Bank to North Carolina	Verrill (1895)	43°19'N, 67°18'W	40°17'N, 68°16'W	83-256	(183-457) ¹ (35-680) ²

¹ Verrill, 1895

² Gray *et al.*, 1968

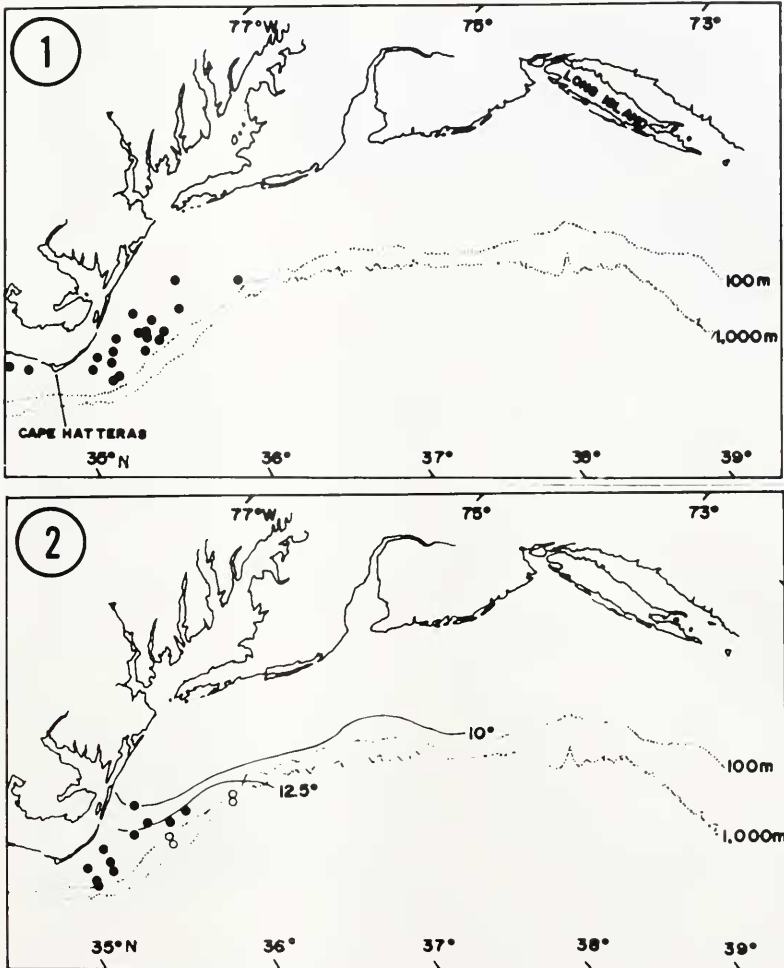


FIGURE 1. Distribution of *Luidia clathrata* on the continental shelf off Cape Hatteras, North Carolina.

FIGURE 2. Distribution of *Astropecten articulatus* (solid circles) and *Stephanasterias gracilis* (open circles) on the continental shelf north of Cape Hatteras in relation to 10°C and 12.5°C February bottom isotherms.

temperatures remain warmer than 7°–8°C (Fig. 7), and where summer bottom isotherms probably do not exceed about 15°C (and are probably less than 10°C over much of the range). The deep-sea red crab (*Geryon quinquidens*) has a similar distribution north of Cape Hatteras, but is known to tolerate water temperatures considerably higher than those encountered in its natural environment (Wigley *et al.*, 1975). This may also be true of *S. tanneri*. It seems likely that winter bottom temperatures are more important than summer temperatures in determining the range of *S. tanneri*.

Odontaster hispidus (Fig. 7) was collected at only two stations off New Jersey and Virginia (Table II).

Porania insignis was taken at a scattering of stations in the central and western

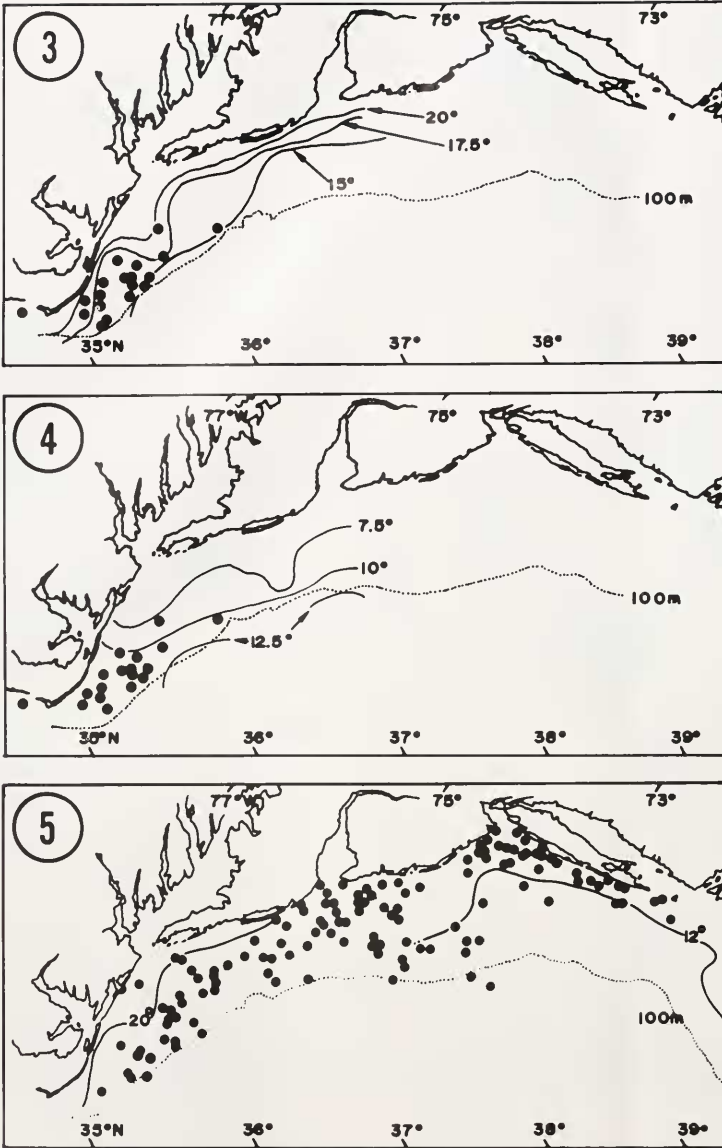


FIGURE 3. Distribution of *Luidia clathrata* in relation to September bottom isotherms, showing absence of correlation between summer temperatures and distribution. This pattern is very similar to *Astropecten articulatus*.

FIGURE 4. Distribution of *Luidia clathrata* in relation to February bottom isotherms. *L. clathrata* collections come from areas where bottom temperatures in winter remain above 7–10°C, a pattern very similar to *Astropecten articulatus*.

FIGURE 5. Distribution of *Asterias forbesi* on the Middle Atlantic continental shelf in relation to the 12° and 20°C September bottom isotherms. *A. forbesi* was sparse inshore of the 20° isotherm south of Virginia (where temperatures may reach or exceed 25°C). Bottom temperatures above 12°C extend northward to Nantucket Shoals and Georges Bank (Fig. 25) although *A. forbesi* is limited to the shelf south of Cape Cod.

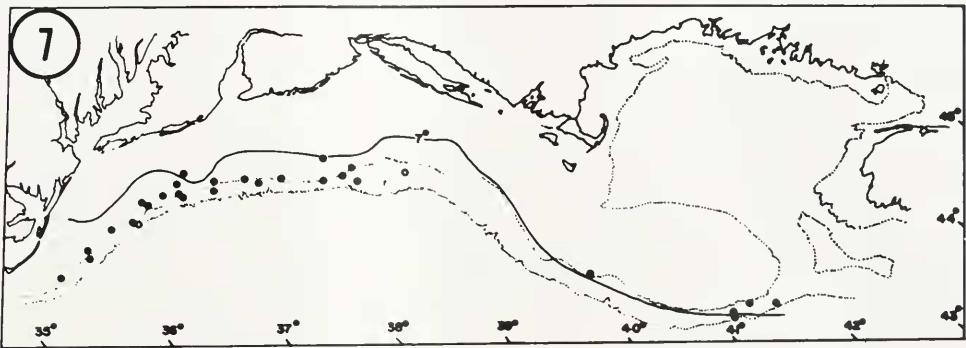
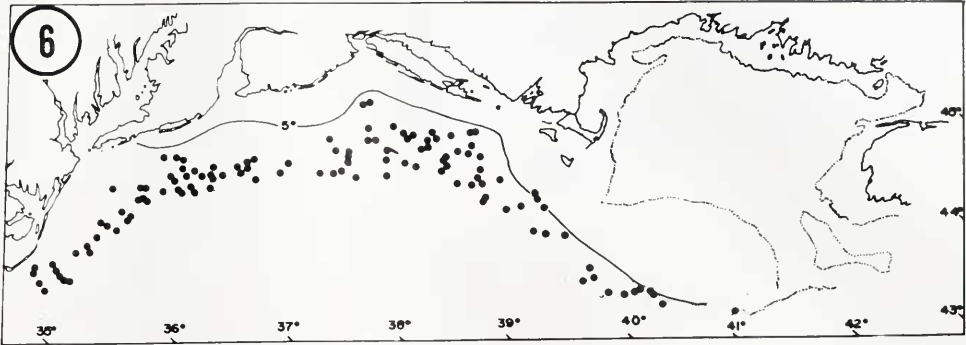


FIGURE 6. Distribution of *Astropecten americanus* in relation to the 5°C February bottom isotherm. Inshore of this isotherm, winter temperatures are less than 5°C.

FIGURE 7. Distribution of *Sclerasterias tanneri* (solid circles) and *Odontaster hispidus* (open circles) in relation to the 7°C February bottom isotherm. Seaward of this isotherm, winter bottom temperatures exceed 7°C.

Gulf of Maine and at the eastern tip of Georges Bank (Fig. 15). Its depth and geographical distribution patterns (Table II) indicate that *P. insignis* is an outer shelf/upper slope species that may track continental slope water into the Gulf of Maine via the Northeast Channel. Fluctuation in bottom temperatures in the observed range of this species is from about 5°C (winter) to around 10°C (summer). Since winter bottom temperatures on the lower shelf and upper slope over the geographical range of *P. insignis* (Georges Bank to North Carolina) range from roughly 8°–12°C, the upper depth limit and northern range limit of this species in the Gulf of Maine probably are determined by winter temperatures in the range of 5°–6°C. Whether or not *P. insignis* is able to reproduce at these temperatures is unknown.

Group 4: Northwest Atlantic subarctic-boreal species (Table III)

The species in the northwest Atlantic subarctic-boreal group, *Asterias vulgaris*, *Leptasterias tenera*, and *Henricia* spp., are confined to the subarctic-boreal zone on the eastern American coast. Their upper (inshore) depth limits become deeper with decreasing latitude (boreal submergence). These species are either very closely

TABLE III

Subarctic-boreal species—present survey.

Species	Geographical range	Reference	Northern limit	Southern limit	Depth range (m)	Previously known depth range (m)
<i>Asterias vulgaris</i> Verrill	Gulf of St. Lawrence (excluding the Strait of Belle Isle) to off Cape Hatteras, North Carolina	Grainger, 1964 Verrill, 1895	44°37'N, 66°10'W	35°22'N, 74°55'W	15–348	0–358
<i>Leptasterias tenera</i> (Stimpson)	45°29' to 37°19'N ^{1,2}	Verrill, 1895	42°57'N, 65°23'W	35°22'N, 74°55'W	31–182	18–236
<i>Henricia</i> spp.	47°29'N to 35°38'N on the coast of the U. S. but extending north into arctic waters ³	Verrill, 1895	44°37'N, 66°10'W	36°52'N, 74°48'W	33–196	0–662 ³

¹ Including *L. compta*, which is generally considered synonymous with *L. tenera*² To southern tip of Greenland according to Mortensen (1932), who suggested that this may represent a recent northern range extension³ For *H. sanguinolenta*

related to Northeastern Atlantic congeners (e.g. *Leptasterias tenera* and *L. muleri*), or are synonymous with European species, e.g. *A. vulgaris* with *A. rubens*; *Henricia* spp. (in part) with *H. sanguinolenta*.

A. vulgaris is evidently morphologically indistinguishable from the European *A. rubens*, justifying the synonymizing of these species (M. E. Downey, personal

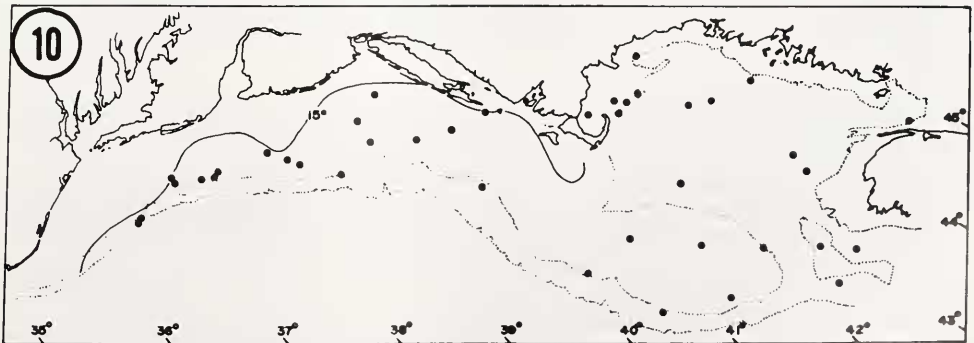
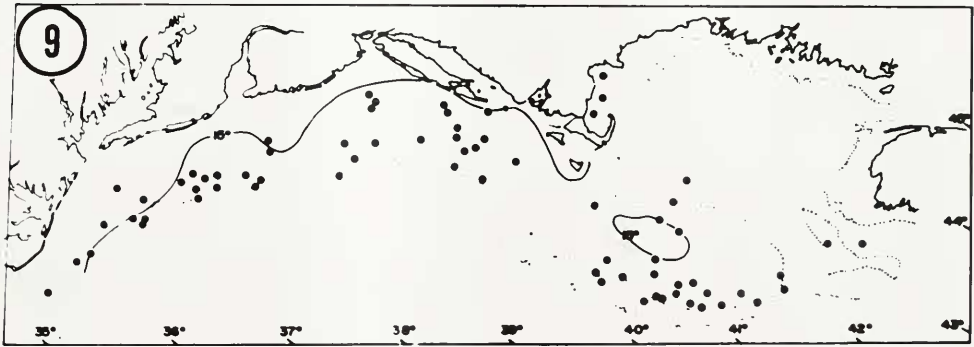
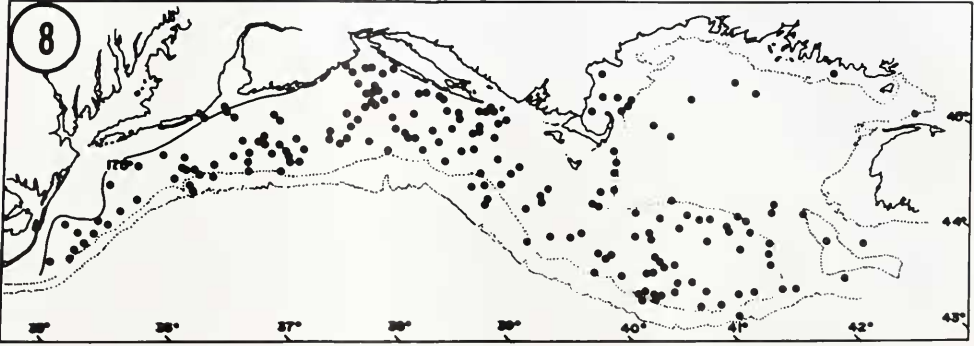


FIGURE 8. Distribution of *Asterias vulgaris*, Gulf of Maine to Cape Hatteras. South of latitude 38°N, distribution is correlated with the 17.5°C bottom isotherm. Inshore of this isotherm, summer bottom temperatures may exceed 17°C.

FIGURE 9. Distribution of *Leptasterias tenera*, Gulf of Maine to Cape Hatteras, in relation to the 15°C September bottom isotherm. Inshore of this isotherm summer bottom temperatures exceed 15°C.

FIGURE 10. Distribution of *Henricia* spp., Gulf of Maine to Cape Hatteras, in relation to the 15°C September bottom isotherm. Inshore of this isotherm summer bottom temperatures exceed 15°C.

communication). However, populations from the Northwest Atlantic may be ecologically and genetically isolated from populations in Iceland and the Northeast Atlantic. Therefore, we have continued to use the name *vulgaris* for American Atlantic populations of *A. rubens*.

A. vulgaris (Figs. 8, 22) occurs over entire breadth of the continental shelf in the zone covered in this survey, from the entrance to the Bay of Fundy south to Maryland. Further south, it is confined to the middle and outer shelf, reaching its southern limit off Cape Hatteras (Table III). The upper (inshore) vertical limit is correlated with summer bottom isotherms of about 17°C. Thus, it would appear that permanent populations of *A. vulgaris* are not found where average summer bottom temperatures exceed this temperature. Winter bottom temperatures corresponding to the observed geographical range vary from near 15°C (off Cape Hatteras) to less than 3°C (Cape Cod Bay, portions of the western Gulf of Maine).

The mechanisms by which temperature controls the southern limits of *A. vulgaris* have not been adequately investigated. In eastern Canada, *A. vulgaris* stops feeding in midsummer (Needler, 1941), and dies when temperatures reach 25°C (Smith, 1940). Clearly, *A. vulgaris* can tolerate temperatures between 17°C and 25°C at least for short periods of time.

The thermal requirements for reproduction of *A. vulgaris* are imperfectly understood, although it is generally recognized as a late spring and summer spawner, with larvae settling from midsummer to autumn (Booolootian, 1966). If all of the points in Figure 22 represent reproducing populations, *A. vulgaris* can occur where summer bottom temperatures reach as low as 6°C. If the records of *A. vulgaris* from the deeper basins of the Gulf of Maine, where bottom temperatures remain at or below 6°C in summer, represent non-breeding animals, the northern limit of *A. vulgaris* would be more closely correlated with summer bottom temperatures of about 8°C. This corresponds to the temperature at which *A. rubens* begins spawning in the White Sea, near the northern range limit of this species (Mileikovsky, 1970). Thus, while the northern limit of *A. vulgaris* may be determined by minimum summer bottom temperatures in the range of 6°–8°C, it is not possible to be more precise, and the effects of temperature on growth, spawning, post-larval development, etc. are unknown. According to Grainger (1964), *A. vulgaris* reaches its northern geographical limits in the Gulf of St. Lawrence, south of the Strait of Belle Isle. Analysis of distribution in relation to seasonal bottom temperatures of this northern population would provide more definitive information on the thermal control of distribution.

Leptasterias tenera is widely distributed on the middle and outer continental shelf from near Cape Hatteras to Brown Bank (off Nova Scotia), and the inner shelf off eastern Long Island, and in Cape Cod Bay (Fig. 9, 23). Hendler and Franz (in preparation) found that in Cape Cod Bay and Block Island Sound, *L. tenera* broods its young from December through March, at bottom temperatures which range from about 3°–7°C. In Block Island Sound, the winter brooding period is followed by a very active feeding period which, however, declines as bottom temperatures rise above 10°–12°C.

The distribution of *L. tenera* is fairly well correlated with the 15°C mean September bottom isotherm (Fig. 9). Average winter bottom isotherms over this area range from 3°–12°C. Thus, warm summer temperatures, probably affecting feeding rate, appear to limit the distribution of *L. tenera*. Since *L. tenera* occurs on the outer shelf and upper slope northeast of Cape Hatteras, it must brood over a large winter temperature range—roughly from 3°–12°C. However, the role of cold winter temperatures in controlling its northward distribution is unclear. Hen-

dlar and Franz (in preparation) noted that the feeding rates of both sexes were lower during January and February. In the Gulf of Maine, *L. tenera* is largely confined to areas in which summer bottom temperatures reach 7°–8°C.

L. tenera is closely related to the European *L. mulleri*, and according to Fisher (1930), at least some of the northwestern Atlantic records of *L. mulleri* may be this species. Grainger (1966) suggested that some specimens identified as *L. mulleri* from the Canadian Atlantic coast may in fact be *L. floccosa*. Clearly, the distribution of *L. tenera* in Canadian Atlantic waters needs to be re-evaluated.

The genus *Henricia* presents confusing nomenclatural and taxonomic problems. *H. sanguinolenta*, a taxon which has been used as a catchall for what may be several Northwest Atlantic species (Grainger, 1966), is a common intertidal species in New England, but undergoes a marked submergence southward (Coe, 1912).

The distribution of *Henricia* spp. (Figs. 10, 24) includes the middle and outer continental shelf from the Gulf of Maine and Georges Bank to off the Virginia coast. The upper (inshore) depth limit drops gradually from north to south, reaching about 50 m at latitude 38°N, and then dropping precipitously to about 150 m at its southern limit. This suggests that the distribution of *Henricia* is limited to areas where summer bottom temperatures do not exceed about 15°C (Fig. 10).

Group 5: Subarctic species (Table IV)

The predominantly subarctic seastars encountered in this survey (Figs. 11–13) were *Hippasteria phygiana*, *Ceramaster granularis*, *Poraniomorpha hispida*, *Psilaster andromeda*, *Leptychaster arcticus*, and *Pseudarchaster parelii*. None of these occurs in arctic waters; in the present study, all were confined to the Gulf of Maine.

These subarctic species extend into very deep waters, although three species were collected in the Gulf of Maine at depths as shallow as 35 m (Table IV). Since the southern geographical limits of all six species are in the Gulf of Maine (excluding continental slope records), thermal limits probably are reached in this area. Summer bottom temperatures corresponding to the distribution patterns of all of the above species do not exceed 7°–8°C, with winter minimum temperatures in the range of 4°C–6°C. Since winter bottom temperatures on nearby Georges Bank are the same as those in the Gulf of Maine, the presence of these species in the Gulf, and their absence from Georges Bank, is probably correlated with summer bottom temperatures.

Group 6: Arctic-subarctic species (Table V)

Six species of seastars, all collected from the Gulf of Maine in this survey, are widely distributed in both arctic and subarctic waters: *Crossaster papposus* (Fig. 14), *Solaster endeca* (Fig. 14), *Ctenodiscus crispatus* (Fig. 15), *Pontaster tenuispinus* (Fig. 15), *Pteraster militaris* (Fig. 16), and *Lophaster furcifer* (Fig. 16).

Both *Crossaster papposus* and *Solaster endeca* occurred in relatively shallow waters compared to other arctic-subarctic species (Table V). *C. papposus* is a predator mostly on asteroids (Feder and Christensen, 1966) and especially on *Asterias* (Mortensen, 1927), and inhabits a wide range of sediments (Grainger, 1966). The concentration of this species on the edge of the continental shelf off Massachusetts Bay, and the eastern tip of Georges Bank (Fig. 14) may reflect a higher biomass of its favored prey.

Summer maximum bottom temperatures corresponding to the observed distri-

TABLE IV

Subarctic species—present survey.

Species	Geographical range	Reference	Southern limit	Depth range (m)	Overall depth range (m)
<i>Hippasteria phrygiana</i> (Parelius)	Cape Cod to Nova Scotia; East and West Greenland to Scotland and England (Channel), Scandinavia from the Kattegat to Finmark	Mortensen, 1927	41°29'N, 66°26'W	35–348	20–800
<i>Ceramaster granulatus</i> (O. F. Muller)	Gulf of Maine to Newfoundland; Southwest Greenland to the Faeroes; Scandinavia from Skagerrak to Finmark; Morocco and Azores; Bering Sea	Grainger, 1966 Mortensen, 1927	42°03'N, 68°27'W	97–197	20–1400
<i>Leptychaster arcticus</i> (M. Sars)	Gulf of Maine to Labrador; West Greenland to Faeroes; Scandinavia from Trondheim to Finmark; Bering Sea to Japan	Verrill, 1895 Mortensen, 1927	41°40'N, 69°33'W	35–196	20–1766
<i>Poraniomorpha hispida</i> (M. Sars)	Off Cape Cod south to 35°12'N (deep water) ¹ ; Southwest Greenland to the Faeroes;	Verrill, 1895 Mortensen, 1927	43°17'N, 69°34'W	135–348	90–1171
<i>Psilaster andromeda</i> (Muller & Troschel)	Skagerrak to northern Norway 38°27'N to 44°47'N ² ; Davis Strait to Ireland; Murman coast to Cape Verdi Islands and Azores	Verrill, 1895 Mortensen, 1932	41°45'N, 69°41'W	35–348	19–1850
<i>Pseudarchaster parelii</i> (Duben & Koren)	37°59'N to 44°26'N ³ ; Southwest Greenland to Ireland, and Barents Sea; Bering Sea to N. Pacific	Verrill, 1895 Grainger, 1966	42°28'N, 66°57'W	318–348	156–2947

¹ As *P. spinulosa* in Verrill (1895). Verrill suggested that *P. spinulosa* was closely related to the European *P. rosea* (*P. hispida*). Mortensen (1932) agreed, as indicated by his citation of Verrill's southern limit of *P. spinulosa* in the general description of the range of *P. hispida*, but Mortensen did not actually cite *P. spinulosa* as a synonym of *P. hispida*.

² In Verrill (1895) as *P. floric*

³ In Verrill (1895) as *P. intermedius* Sladen

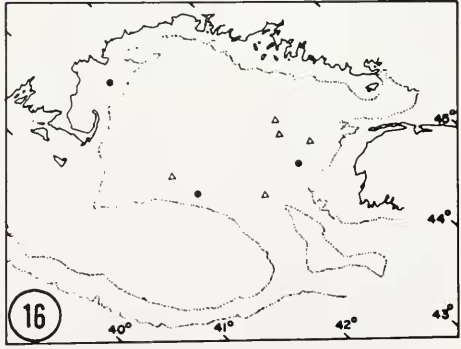
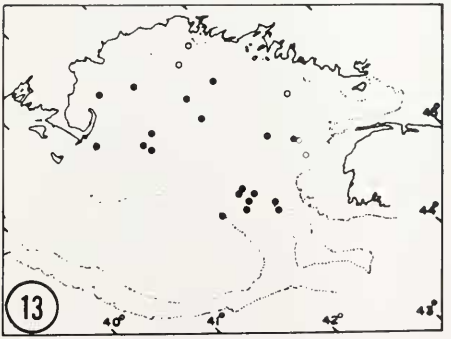
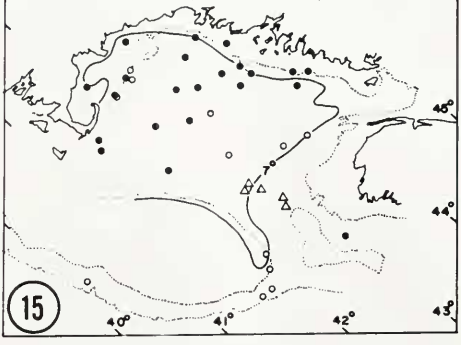
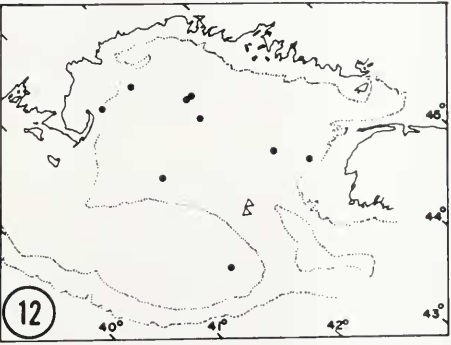
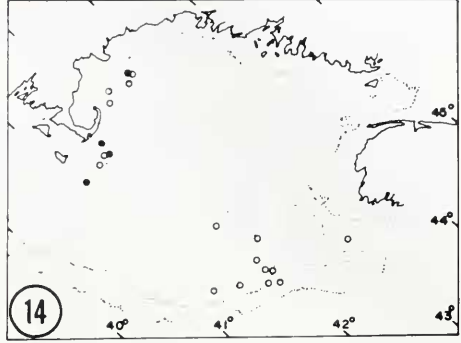
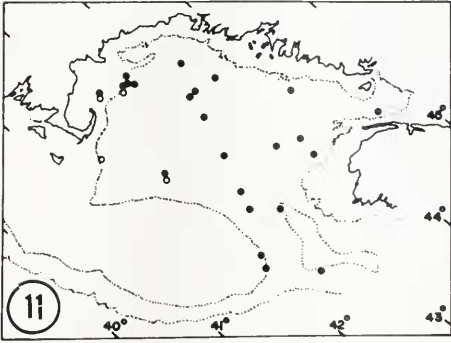


FIGURE 11. Distribution of *Hippasteria phrygiana* (solid circles) and *Leptychaster arcticus* (open circles) in the Gulf of Maine.

FIGURE 12. Distribution of *Pseudarchaster parelii* (open triangles) and *Ceramaster granularis* (solid circles) in the Gulf of Maine.

FIGURE 13. Distribution of *Poraniomorpha hispida* (open circles) and *Psilaster andromeda* (solid circles) in the Gulf of Maine.

FIGURE 14. Distribution of *Crossaster papposus* (open circles) and *Solaster endeca* (solid circles) in the Gulf of Maine.

FIGURE 15. Distribution of *Ctenodiscus crispatus* (solid circles), *Pontaster tenuispinus* (open triangles), and *Porania insignis* (open circles) in the Gulf of Maine. The 7°C September bottom isotherm is superimposed.

FIGURE 16. Distribution of *Pteraster militaris* (open triangles) and *Lophaster furcifer* (solid circles) in the Gulf of Maine.

TABLE V

Arctic-subarctic species—present survey.

Species	Range	References	Southern limit	Depth range (m)	Overall depth range (m)
<i>Crossaster papposus</i> (L)	North Pacific; Bering Sea, Arctic Ocean, NW Atlantic south to the Gulf of Maine; NE Atlantic south to England	Grainger, 1966	41°16'N, 66°34'W	35-186	0-1200
<i>Solaster endeca</i> (L)	North Pacific to Vancouver and the Okhotsk Sea; Bering Sea; Arctic Ocean; E. Canada south to Cape Cod; NE Atlantic south to England	Mortensen, 1927	41°15'N, 69°25'W	48-129	48-450
<i>Ctenodiscus crispatus</i> (Retzius)	North Pacific; Bering Sea; Arctic Ocean; Canadian Arctic south to Gulf of Maine; NE Atlantic south to Faroes and Trondheim	Mortensen, 1927 Grainger, 1966	41°40'N, 69°33'W	49-227	2-1900
<i>Pontaster tenuispinus</i> (Duben & Koren)	Arctic Ocean from NE Canada to East Siberian Sea; NW Atlantic south to Nova Scotia; NE Atlantic south to Faroes, but not North Sea	Verrill, 1895 Grainger, 1966	42°33'N, 67°17'W	154-293	20-1960
<i>Pteraster militaris</i> (O. F. Muller)	North Pacific south to Vancouver and Japan; Bering Sea; Arctic Canada to Chukchi Sea; NW Atlantic south to Massachusetts Bay; NE Atlantic south to Faroes and Skagerrak	Verrill, 1895 Grainger, 1966	42°03'N, 68°27'W	91-267	10-1100
<i>Lophaster furcifer</i> (Duben & Koren)	North Pacific (as <i>L.f. vexator</i>) to California and Japan; Arctic Ocean from NW Canada to Laptev Sea; NW Atlantic to Gulf of Maine; NE Atlantic to Faroe Channel	Verrill, 1895 Mortensen, 1927 Grainger, 1966	42°07'N, 67°55'W	49-200	30-1350

bution of *C. papposus* and *S. endeca* in the Gulf of Maine and eastern Georges Bank range from 8°–10°C. In Europe, *S. endeca* is said to tolerate summer temperatures up to 14°C (Ursin, 1960).

Ctenodiscus crispatus is a mud dweller that feeds on organic detritus (Mortensen, 1927). In the Gulf of Maine, it occurs on clay to silty sand bottoms where organic contents are probably greater than 0.5% (based on sediment data from Hayes and Wigley, 1969). Mortensen (1927) reported that *C. crispatus* could live at temperatures up to 10°C in Scandinavia. In the present study, its distribution corresponded to maximum summer temperatures of roughly 7°C (Fig. 15).

Pontaster tenuispinus and *Pteraster militaris* were restricted to relatively few, generally deep, stations in the eastern and southeastern basins of the Gulf of Maine where summer bottom temperatures remain at or below 7°–8°C. Similarly, the distribution pattern of *Lophaster furcifer* was associated with bottom temperatures not exceeding 7°–8°C. The relationship between the combined distribution patterns of all of the arctic-subarctic species recorded in this survey, and summer bottom temperatures (Fig. 25) indicates that arctic-subarctic species are not found where bottom temperatures rise much above 8°–9°C.

DISCUSSION

Temperature control of distribution

Temperature may limit the distribution of species by affecting survival, reproduction, development of juveniles, and biotic interactions (competition, predation, and disease). It may influence any stage of the life cycle (Krebs, 1978). Few of the experimental studies necessary to prove decisively that temperature limits distribution have been carried out on seastars. Independent information on the influence of temperature on physiological rates (feeding, reproduction), and survival is available for only a few of the species in the continental shelf zone of the Middle Atlantic.

Investigations demonstrating a correlation between environmental temperature and geographical distribution are frequently used to indicate thermal control, and to suggest the ways in which temperature may act in controlling distribution. A well known model that attempts to account for temperature regulation of the latitudinal distribution of benthic marine invertebrates is that of Hutchins (1947), who proposed that temperature controls species through its effects on survival and/or reproduction (repopulation). His analysis requires the correlation of latitudinal distribution of species with seasonal minimum and maximum seawater temperatures. We have not applied Hutchins' procedures to the species distributions of seastars, primarily because the survival/reproduction dichotomy provides little information on the actual mechanisms of thermal control.

Thermal control of distribution of Asterias forbesi and Asterias vulgaris

Several aspects of the depth and latitudinal ranges of the common seastars *Asterias forbesi* and *Asterias vulgaris* merit further discussion, and provide the basis for speculations concerning the thermal control of distribution in these species. The feeding rate of *A. forbesi* in Long Island Sound declines above 22°C, and at 25°C animals rapidly lose weight, although feeding continues (MacKenzie, 1969). Thus, the scarcity of *A. forbesi* on the inner continental shelf off the Virginia and North Carolina coasts may be correlated with summer bottom temperatures higher than 20°C (Fig. 5).

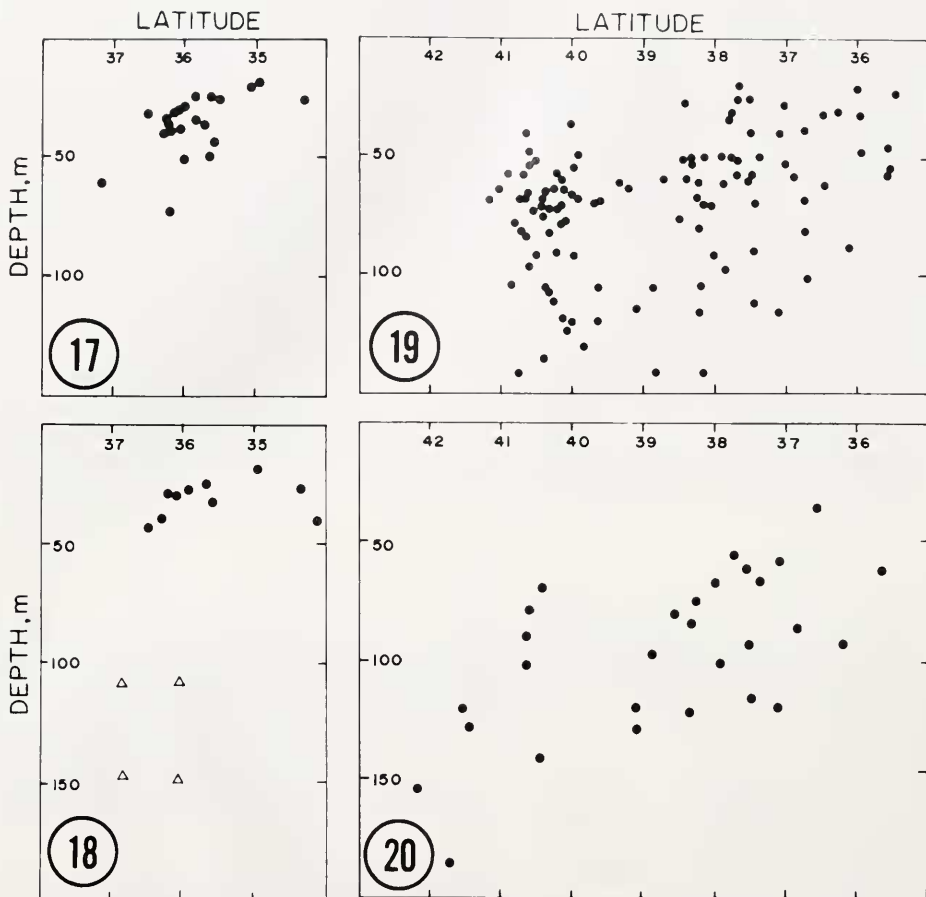


FIGURE 17. Depth distribution of *Luidia clathrata* on the continental shelf, showing northward submergence.

FIGURE 18. Depth distribution of *Stephanasterias gracilis* (open triangles) and *Astropecten articulatus* (closed circles). The latter, like *Luidia clathrata*, exhibits northward submergence.

FIGURE 19. Depth distribution of *Astropecten americanus*. The upper (inshore) depth limits undergo northward submergence.

FIGURE 20. Depth distribution of *Sclerasterias tanneri*. Like *Astropecten americanus*, *S. tanneri* exhibits northward submergence.

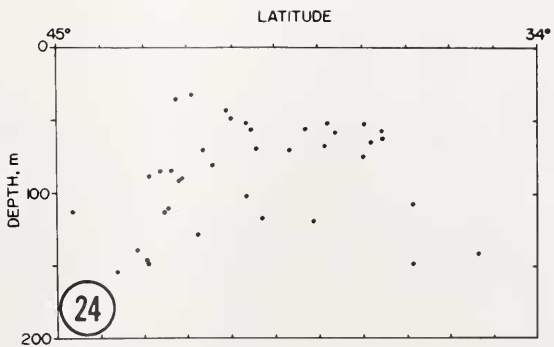
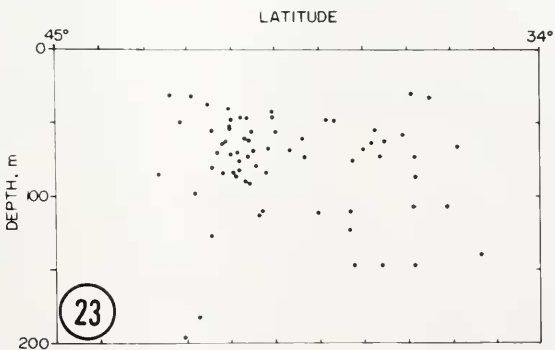
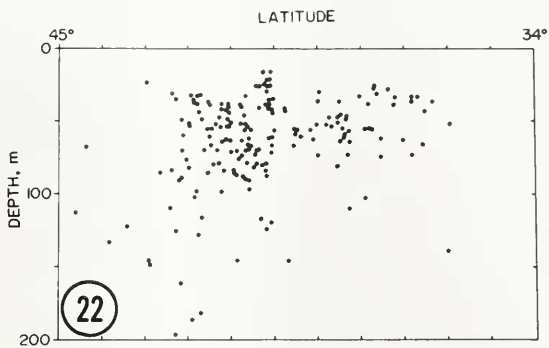
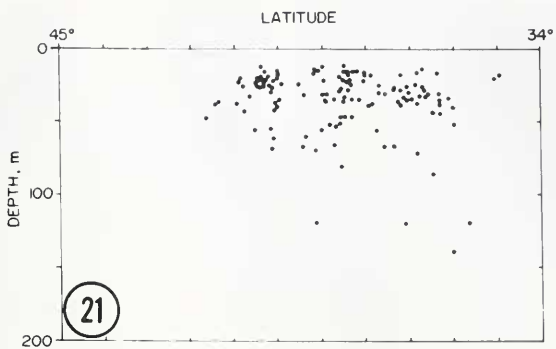
In Long Island Sound, *A. forbesi* reproduces at 15°–16°C (Galtsoff and Loosanoff, 1939; Loosanoff, 1961). If this applies to offshore populations as well, then collections in Figure 21 from the outer continental shelf, south of 40°N, may represent "pseudopopulations" in the sense of Mileikovsky (1971), *i.e.* non-breeding

FIGURE 21. Depth distribution of *Asterias forbesi*. The upper (inshore) depth limits do not submerge to the south although the lower (offshore) depth limits increase southward.

FIGURE 22. Depth distribution of *Asterias vulgaris*. The upper (inshore) depth limits undergo submergence with decreasing latitude, the phenomenon of "boreal submergence." The lower (offshore) depth limits appear to rise into shallower waters with decreasing latitude.

FIGURE 23. Depth distribution of *Leptasterias tenera* on the Middle Atlantic continental shelf.

FIGURE 24. Depth distribution of *Henricia spp.*, Gulf of Maine to Cape Hatteras. The upper (inshore) depth limits undergo submergence with decreasing latitude ("boreal submergence").



aggregations which result from larvae settling at depths where bottom temperatures remain too low for gametogenesis and/or spawning.

Bottom temperatures on portions of the inner continental shelf off eastern Long Island, Nantucket Shoals, and portions of Georges Bank approach 15°C during August and September (Colton and Stoddard, 1973). Thus, it seems likely that *A. forbesi* larvae settle in these areas. However, *A. forbesi* did not occur in our collections, although *A. vulgaris* was abundant (cf. Figs. 5, 8). This absence may be caused by suboptimal feeding temperatures on Nantucket Shoals and portions of Georges Bank, perhaps coupled with competition between *A. forbesi* and *A. vulgaris*. The optimum temperature for feeding in *A. forbesi* is 20°C, and feeding ceases altogether at about 5°C (Zinn, 1937; MacKenzie, 1969), whereas *A. vulgaris* probably continues to feed even at temperatures as low as 3°C (Hancock, 1955). Since winter bottom temperatures remain above 3°C but below 5°C over much of Georges Bank and Nantucket Shoals (Colton and Stoddard, 1973), *A. vulgaris* may continue feeding, a competitive advantage over dormant *A. forbesi*. Furthermore, since optimum feeding temperatures of *A. vulgaris* are probably lower than those for *A. forbesi*, bottom temperatures during the summer months would probably be more favorable for *A. vulgaris* than for *A. forbesi*. Thus, *A. vulgaris* may enjoy a competitive advantage during all seasons. If these speculations are valid, *A. forbesi* is excluded from these large and highly productive areas where, in the absence of competition, it could survive and possibly reproduce.

Depth distribution patterns support the hypothesis that interactions other than direct thermal control determine the distribution of *A. forbesi*. While *A. forbesi* is most common in shallow water (<30m) throughout its range, its lower vertical range increases southward (Fig. 21). Since bottom temperatures at intermediate depths (50–100 m) become progressively warmer with decreasing latitude, the increasing depth range may merely indicate a seaward shift in the bottom temperatures suitable to the survival of *A. forbesi*. However, as summer bottom temperatures increase, *A. forbesi* juveniles are at a lesser competitive disadvantage relative to *A. vulgaris*. Thus, nonbreeding populations of *A. forbesi* may co-exist with adult *A. vulgaris* at depths in which seasonal changes in bottom temperatures do not clearly favor either species.

The upper (vertical) depth limit of *A. vulgaris* decreases and its lower depth limit rises in a gradient from north to south (Fig. 22). A declining upper vertical limit (submergence) reflects *A. vulgaris*' intolerance of warm summer conditions on the inner continental shelf, and possibly a competitive disadvantage vis-a-vis *A. forbesi*. The shallower lower-depth limit toward the south is not easily explained. Hutchins' (1947) model predicts that eurythermal cold-water species limited in their southward distribution by the effects of warm temperatures on reproduction should emerge southward, since winter temperatures suitable for reproduction will occur in progressively shallower waters to the south. However, this cannot account for the observed patterns in *A. vulgaris*, because summer bottom temperatures at depths ≥ 100 m are generally between 10°C and 17°C, a favorable temperature range for *A. vulgaris*. Two factors that may affect the success of *A. vulgaris* at moderate depths are competition with *A. forbesi* and recruitment. The lower depth limit of *A. forbesi* becomes deeper over the same depth and latitudinal range in which *A. vulgaris* becomes shallower. Perhaps the relatively warm winter conditions, and warmer summer bottom temperatures south of 38°N favor *A. forbesi* over *A. vulgaris*. The recruitment of *A. forbesi* in this zone might also be favored over *A. vulgaris*. Southward-flowing long-shore currents along the Virginia/North Carolina coastal shelf are deflected northeasterward inshore of the northeasterward-flowing Gulf Stream (Ford and Miller, 1952). Thus, recruitment of *Asterias* spp.

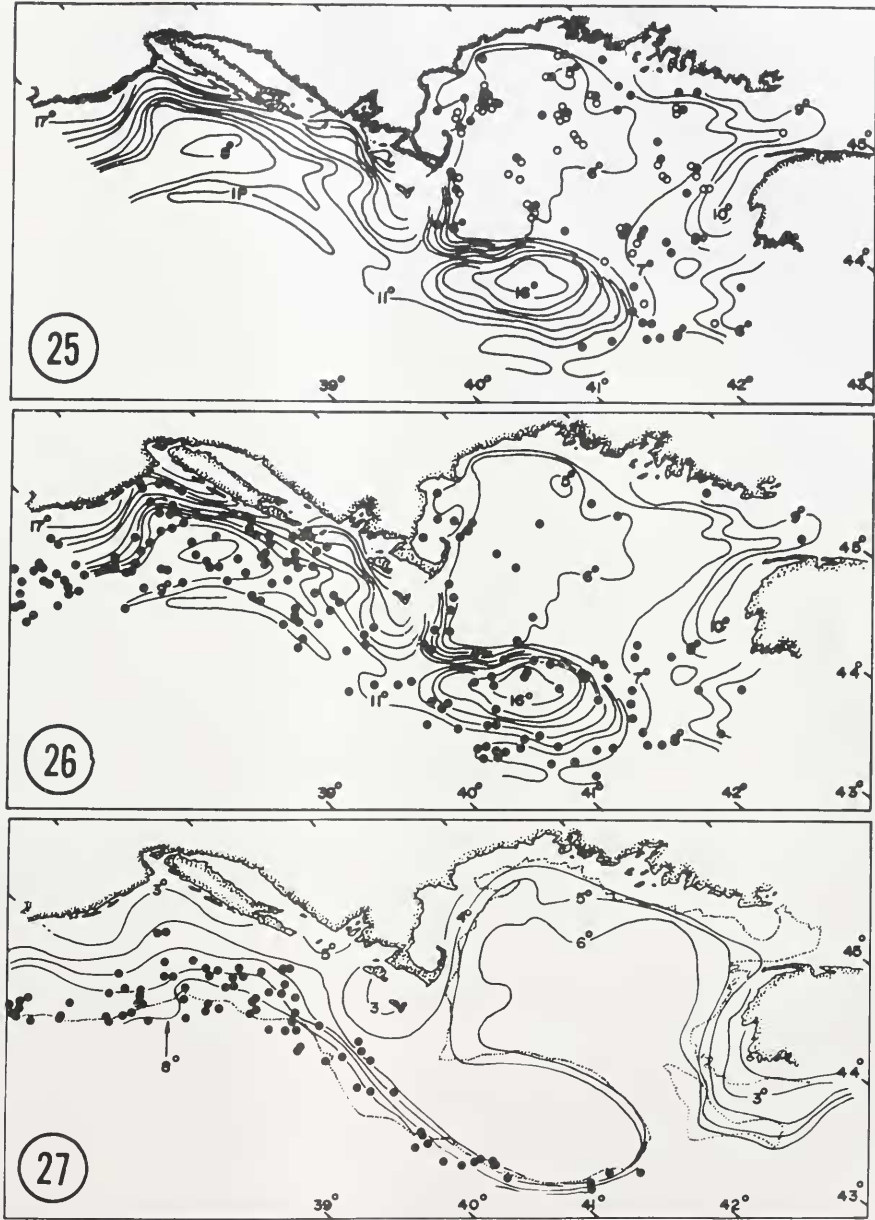


FIGURE 25. Distribution of all arctic-subarctic (open circles) and subarctic (solid circles) species in relation to September bottom isotherms, Gulf of Maine to Cape May (New Jersey). Compressed isotherms associated with Nantucket Shoals and Georges Bank constitute a sharp thermal barrier to the southward distribution of these species.

FIGURE 26. Distribution of all subarctic-boreal species (excluding *Henricia* spp.) in relation to September bottom isotherms, Gulf of Maine to Cape May (New Jersey). Note that subarctic-boreal species are not constrained in their distribution by bottom temperatures in the Gulf of Maine, and are thus relatively immune to the effects of the strong thermal barrier associated with Georges Bank and Nantucket Shoals.

FIGURE 27. Distribution of all boreal outer shelf species in relation to February bottom isotherms, Gulf of Maine to Cape May (New Jersey). Winter temperatures on the inner continental shelf and Georges Bank prevent the northward extension of these species.

on the outer continental shelf just north of Cape Hatteras probably depends on populations of larvae carried by these currents. Many more *A. forbesi* larvae probably are entrained by such currents than larvae of *A. vulgaris*, because of the relative scarcity of *A. vulgaris* on the inner continental shelf off North Carolina and Virginia.

Faunal groups of continental shelf seastars

The six faunal groups of seastars proposed above are based on similarities in depth and latitudinal distribution patterns, and similarities in temperature-distribution correlations. We suggest that these faunal groups represent more than random aggregations of animals with similar physiological requirements. They may also share similar paleobiogeographical patterns, such as similar origins in space, and presence in the Northwest Atlantic for comparable lengths of time. Direct evidence relating to the paleobiogeography of North Atlantic asteroids is lacking, so hypotheses based on this approach must depend, at least for the present, on analogies between faunal patterns in seastars and testaceous invertebrate taxa such as Mollusca and Foraminifera, for which fossil records already exist.

Franz and Merrill (1980a, b) suggested that warm-water mollusks with geographical ranges that extend north of Cape Hatteras (the "transhatteran" fauna) are derived from the Miocene fauna of the North Atlantic, and characteristically range southward to Florida, the Gulf of Mexico, and the Caribbean. Although *A. forbesi* does occur southward to the Florida Keys, and was reported by Verrill (1895) in the northern Gulf of Mexico, a review of distributional records in the collections of the United States National Museum suggests that it is rare south of the Cape Kennedy/Melbourne area. It is absent from museum collections from the Gulf of Mexico. Similarly, the records listed by Downey (1973) in her monograph of Caribbean and Gulf of Mexico starfish are all from the east coast of Florida north of latitude 28°N. These data indicate that while *A. forbesi* ranges south of the Cape Hatteras thermal barrier, its southern limits seem to be the eastern coast of Florida: it may occur rarely or not at all in the Gulf of Mexico. In this regard, its distribution pattern is different from those exhibited by most continental shelf transhatteran species of mollusks.

A. forbesi is closely related to *A. vulgaris* (Schopf and Murphy, 1973), *A. rubens*, and *A. amurensis* (Fisher, 1930), all species of the North Atlantic or the North Pacific. Worley and Franz (in preparation) hypothesize that these species share a common North Pacific ancestor and that this genus entered the North Atlantic via the Arctic in the late Miocene or Pliocene. If so, the transhatteran pattern of *A. forbesi* is not evidence of a Miocene Atlantic ancestry, but nevertheless reflects a relatively long period of adaptation to the marine climate of the Northwest Atlantic.

Franz and Merrill (1980b) postulate that the endemic boreal component of the molluscan shelf fauna comprises species either of Miocene Atlantic progenitors, or species of North Pacific origin, but with long evolutionary histories in the North Atlantic. The seastars of Group 3, the Northwest Atlantic outer shelf boreal species, would appear to fit the former pattern. The genera *Sclerasterias*, *Astropecten*, and *Porania* are predominantly warm-water cosmopolitan (Fisher, 1911, 1928). All of the species of this group are endemic to the boreal zone of the Northwest Atlantic, and all of the genera are characterized by a marked diversification south of Cape Hatteras. Thus, these genera probably have ancient (pre-miocene) Atlantic or Tethyan origins.

The species of Group 4, with geographical ranges including the boreal zone and extending into subarctic waters, and exhibiting boreal submergence, are similar to the amphiatlantic component of the boreal mollusks described by Franz and Merrill (1980a, b). The two seastars *Asterias vulgaris* and *Leptasterias tenera* are closely related to the Northeastern Atlantic congeners *A. rubens* and *L. mulleri*. All of these species are unquestionably of northern origin, with closest relatives in the subarctic Atlantic, the Arctic Ocean, Bering Sea, and boreal North Pacific. The progenitors of *L. tenera* and *A. vulgaris* probably entered the Atlantic via the Arctic (Nesis, 1961) in the Pliocene, and these species evolved separately in the Northeast and Northwest Atlantic during the Pliocene and Pleistocene.

Groups 5 and 6, the subarctic and arctic-subarctic species, are similar in being entirely amphiatlantic, and in their generally eurybathic depth ranges (Tables IV, V). Three of the species of Group 5 are not found in the Bering Sea or North Pacific, although *Hippasteria phrygiana* is closely related to the North Pacific *H. spinosa* (Nesis, 1961). According to Grainger (1966), *Ceramaster granularis* occurs in the Bering Sea while *Leptychaster arcticus* and *Pseudorchaster parelii* are found in the Bering Sea and the Northwest Pacific. All three species have discontinuous Atlantic-Pacific distributions, *i.e.*, they are present in the North Atlantic and North Pacific but absent from the Arctic Ocean. In a recent analysis of the Mollusca of the Western Beaufort Sea, Bernard (1979) indicated that 13 of 24 species of probable Atlantic origin do not extend into the Bering Sea; and that only 1 of 21 species of probable Pacific origin does not occur now in the Bering Sea. This implies that the Group 5 fauna may be of mixed origins, including genera with Atlantic origins (*Poraniomorpha*, *Psilaster*) and Pacific origins (*Hippasteria*, *Ceramaster*, *Leptychaster*, *Pseudarchaster*). The latter were probably distributed continuously when the Arctic was slightly warmer than at present (Mortensen, 1932; Ekman, 1953; Nesis, 1961), or evolved from progenitors that migrated from the North Pacific.

The Bering Strait may have opened and closed several times in the late Miocene, Pliocene, and Pleistocene (Hopkins, 1973). When the Strait was open, animals migrated between the North Pacific, Arctic, and Atlantic (Nesis, 1961). Thus, several waves of immigration of Pacific species into the Arctic and into the Atlantic (and vice versa) would have taken place. The earliest immigrants, because of their longer history in the North Atlantic, would be expected to show the greatest divergence from their North Pacific congeners. Most of the subarctic species of Group 5 exemplify this pattern, *i.e.* species which evolved in the Atlantic from early transarctic migrants. Eastern and western Atlantic species also would become differentiated during the Pliocene as populations became better adapted to the rather rapidly changing environments of the Northwest and Northeast Atlantic. The disappearance of connectant populations along the North Atlantic Arc, as glacial conditions developed in Greenland and Iceland in the Pliocene, probably facilitated speciation. Pairs of related species such as *Asterias forbesi* and *A. rubens*, and *Leptasterias tenera* and *L. mulleri*, may have differentiated in the North Atlantic by this process.

Species that now have continuous Arctic distribution patterns, but that extend their ranges into the North Atlantic and into the North Pacific, would be expected to exhibit less regional morphological differentiation, and to be less well adapted to the specific environment of the northwest Atlantic shelf. The arctic-subarctic species of Group 6 may represent this pattern.

If our hypotheses are valid, the origins of the continental shelf asteroid fauna of the Northwest Atlantic are complex. The fauna is composed of a mixture of

groups of different origins in time, and various degrees of specific differentiation, probably resulting from sporadic transarctic migrations. We reached the same conclusions in our analysis of molluscan distribution patterns. However, one major discrepancy between mollusks and asteroids is apparent. While the shallow shelf and shore molluscan fauna between Cape Hatteras and Cape Cod is dominated by species of Miocene/Pliocene Atlantic origins (the transhatteran fauna), the diversity of seastars occupying this zone is extremely low. South of Cape Hatteras seastar diversity increases nearshore and on the continental shelf, an increase accounted for by additional endemic subtropical-tropical taxa. The absence of a transhatteran component of endemic, warm-water starfish—a faunal group very prominent in the mollusks—is unexplained. The answer may lie in the character of the Miocene shore environment of the East Coast of North America, dominated as it probably was by shallow embayments and great estuaries relatively non-conducive to asteroid diversification.

Faunal barriers

The distribution patterns of seastars re-emphasize an important point: for continental shelf species, Cape Hatteras and Cape Cod, *per se*, are not barriers. Thermal discontinuities associated with the confluence of surface currents, and influenced by the configurations of the continental shelf, are barriers to the distribution of some faunal groups. As noted earlier, the northward ranges of *Luidia clathrata*, *Astropecten articulatus*, and *Stephanasterias gracilis* are not directly affected by the geophysical presence of Cape Hatteras, but by the seasonal chilling of inshore waters north of Cape Hatteras under the influence of the coastal longshore currents. This is also true of the Cape Cod region. The major faunal barriers observed in this study are thermal, associated with the compression of bottom isotherms along the margins of Georges Bank and Nantucket Shoals. This is illustrated in Figures 25 and 26, which show the distribution of arctic-subarctic, subarctic, and subarctic-boreal species (excluding *Henricia*) superimposed on September bottom isotherms. Note that the range limits of both the arctic-subarctic and subarctic faunal groups are closely correlated with the compressed summer bottom isotherms associated with Nantucket Shoals and the northern slope of Georges Bank (as noted also for ostracods by Hazel, 1970, polychaetes by Kinner, 1977, and amphipods by Watling, 1979). However, the subarctic-boreal species are not affected by these isotherms and extend their ranges across Georges Bank and into the Gulf of Maine. The outer shelf boreal group (Fig. 27) is also limited by compressed isotherms; but in this case by winter isotherms associated with the southern slope of Georges Bank. Winter bottom temperatures on Georges Bank and on the northern slope (4°–6°C) inhibit the northward extension of these species.

ACKNOWLEDGMENTS

We gratefully acknowledge the unstinting assistance and cooperation of the personnel of the National Marine Fisheries Service at both Woods Hole and Sandy Hook. Dr. M. J. Cerase-Vivas identified all of the seastars from Cruise 60-7. We thank Dr. Ailsa Clark of the British Museum of Natural History, and Maureen Downey of the Echinoderm Division, United States National Museum, for their assistance in identifying certain specimens. Maureen Downey kindly confirmed all of our identifications. We also thank Dr. Gordon Hendler, Smithsonian Sorting Center, for constructive comments on this manuscript. This research was supported

in part by a grant from the City University of New York (PSC-CUNY Grant No. 13315).

LITERATURE CITED

- BERNARD, F. R. 1979. Bivalve mollusks of the Western Beaufort Sea. *Contrib. Sci. Nat. Hist. Mus. Los Angeles County* **313**: 1-80.
- BOOLOOTIAN, R. A. 1966. Reproductive Physiology. Pp. 561-614 in R. A. Boolootian, Ed., *Physiology of Echinodermata*. Interscience, New York.
- BOWMAN, M. J., AND L. D. WUNDERLICH. 1977. Hydrographic properties. *MESA New York Bight Atlas I*, New York Sea Grant Inst., Albany, N. Y. 78 pp.
- CLARK, H. L. 1904. The echinoderms of the Woods Hole Region. *Fish. Bull. U. S. Fish Wildl. Serv.* **1902**: **22**: 545-576.
- COE, W. R. 1912. Echinoderms of Connecticut. Bull. 19, *Conn. Geol. Nat. Hist. Surv.* Hartford, CT. 152 pp.
- COLTON, J. B., AND R. R. STODDARD. 1973. Bottom-water temperatures on the continental shelf, Nova Scotia to New Jersey. *NOAA Tech. Rept. NMFS Circ-376*. 55 pp.
- DOWNEY, M. E. 1973. Starfishes from the Caribbean and the Gulf of Mexico. *Smithsonian Contr. Zool.* **126**: 158 pp.
- DUNBAR, M. J. 1951. Eastern Arctic waters. *Bull. Fish. Res. Bd. Can.*, **88**. 131 pp.
- DUNBAR, M. J. 1953. Arctic and subarctic marine ecology: immediate problems. *Arctic* **6**(2): 75-90.
- EKMANN, S. 1953. *Zoogeography of the Sea*. Sidgwick & Jackson, London. 417 pp.
- FEDER, H. M., AND A. M. CHRISTENSEN. 1966. Aspects of asteroid biology. Pp. 88-127 in R. A. Boolootian, Ed., *Physiology of Echinodermata*. Interscience, New York.
- FISHER, W. K. 1911. Asteroidea of the North Pacific and adjacent waters. Pt. 1. Phanerozonia and Spinulosa. *Bull. U. S. Nat. Mus.* **76**. 419 pp.
- FISHER, W. K. 1928. Asteroidea of the North Pacific and adjacent waters. Pt. 2. Forcipulata (part). *Bull. U. S. Nat. Mus.* **76**. 245 pp.
- FISHER, W. K. 1930. Asteroidea of the North Pacific and adjacent waters. Pt. 3. Forcipulata. *Bull. U. S. Nat. Mus.* **76**. 356 pp.
- FORD, W. L., AND A. R. MILLER. 1952. The surface layer of the Gulf Stream and adjacent waters. *J. Mar. Res.* **11**: 267-280.
- FRANZ, D. R., AND A. S. MERRILL. 1980a. Molluscan distribution patterns on the continental shelf of the Northwest Atlantic. *Malacologia* **19**(2): 209-225.
- FRANZ, D. R., AND A. S. MERRILL. 1980b. The origins and determinants of distribution of molluscan faunal groups on the shallow continental shelf of the Northwest Atlantic. *Malacologia* **19**(2): 227-248.
- GALTSOFF, P. S., AND V. J. LOOSANOFF. 1939. Natural history and methods controlling the starfish (*Asterias forbesi* Desor). *Bull. U. S. Bur. Fish.* **49**(31): 75-132.
- GRAINGER, E. H. 1964. Asteroidea of the "Blue Dolphin" expedition to Labrador. *Proc. U. S. Nat. Mus.* **114**(3478): 31-46.
- GRAINGER, E. H. 1966. Sea Stars (Echinodermata: Asteroidea) of arctic North America. *Bull. Fish Res. Bd. Com.* **152**. 70 pp.
- GRAY, I. E., M. DOWNEY, AND M. J. CERAME-VIVAS. 1968. Sea stars of North Carolina. *U. S. Fish. Wildl. Serv. Fish. Bull.* **67**(1): 127-163.
- HALL, C. A. 1964. Shallow-water marine climates and molluscan provinces. *Ecol.* **45**(2): 226-234.
- HANCOCK, D. A. 1955. The feeding behavior of starfish on Essex oyster beds. *J. Mar. Biol. Assoc. U. K.* **34**: 313-331.
- HAYNES, E. B., AND R. L. WIGLEY. 1969. Biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. *Trans. Am. Fish. Soc.* **98**(1): 60-76.
- HAZEL, J. E. 1970. Atlantic continental shelf and slope of the United States—Ostracode Zoogeography in the southern Nova Scotian and northern Virginian faunal provinces. *U. S. Geol. Surv. Prof. Pap.* **S29-E**. 21 pp.
- HOPKINS, D. M. 1973. Sea level history in Beringia during the past 250,000 years. *Quat. Res.* **3**: 520-540.
- HUTCHINS, L. W. 1947. The basis for temperature zonation in geographical distribution. *Ecol. Monogr.* **17**: 325-335.
- KINNER, P. C. 1977. The distribution and ecology of errantiate polychaetes on the continental shelf from Cape Cod to Cape Hatteras. *M. S. Thesis, Univ. Delaware*. 122 pp.

- KREBS, C. J. 1978. *Ecology: The experimental analysis of distribution and abundance*. Harper & Row, New York. 678 pp.
- LOOSANOFF, V. L. 1961. Biology and methods of controlling the starfish, *Asterias forbesi* (Desor). *U. S. Fish Wildlf. Bur. Fish. Leaflet* **520**. 11 pp.
- MACKENZIE, C. L. 1969. Feeding rates of starfish, *Asterias forbesi* Desor at controlled temperatures and during different seasons of the year. *U. S. Fish. Wildl. Serv.* **68(1)**: 67-72.
- MILEIKOVSKY, S. A. 1970. Seasonal and daily dynamics in pelagic larvae of marine and shelf bottom invertebrates in nearshore waters of Kandalaksha Bay (White Sea). *Mar. Biol.* **5**: 180-194.
- MILEIKOVSKY, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* **10(3)**: 193-213.
- MORTENSEN, T. 1927. *Handbook of the echinoderms of the British Isles*. Oxford Univ. Press, London. 471 pp.
- MORTENSEN, T. 1932. Echinoderms. The Godthaab Expedition 1978. *Medd. om Grönland.* **79(2)**: 62 pp.
- NEEDLER, A. W. H. 1941. Oyster farming in Canada. *Bull. Fish. Res. Bd. Can.* **60**: 83 pp.
- NESIS, K. N. 1961. The routes and periods of formation, of the interrupted area of distribution of amphiboreal species of marine bottom animals. *Okeanologiya* **1(5)**: 894-903.
- SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* **102**: 243-282.
- SANDERS, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symposium on Biology* **22**: 71-81.
- SCHOPF, T. J. M., AND L. S. MURPHY. 1973. Protein polymorphism of the hybridizing seastars *Asterias forbesi* and *Asterias vulgaris* and implications for their evolution. *Biol. Bull.* **145**: 587-597.
- SMITH, G. F. M. 1940. Factors limiting distribution and size in starfish. *J. Fish Res. Bd. Can.* **5**: 84-103.
- URSIN, E. 1960. A quantitative investigation of the echinoderm fauna of the central North Sea. *Medd. Danm. Fisk-Havunders* **2**: 1-104.
- VERRILL, A. E. 1878. Notice of recent additions to the marine fauna of the eastern coast of North America. *Am. J. Sci.* **16**: 207, 231.
- VERRILL, A. E. 1894. Descriptions of new species of starfish and ophiurans. *Proc. U.S. Nat. Mus.* **17**: 245-297.
- VERRILL, A. E. 1895. Distribution of the echinoderms of Northeastern America. *Am. J. Sci. Ser. 3, XLII (Arts 13, 19)*: 127-141, 199-212.
- WALFORD, L. A., AND R. I. WICKLUND. 1968. Monthly sea temperature structure from the Florida Keys to Cape Cod. *Ser. Atlas Mar. Environ. Am. Geogr. Soc.* **(15)**: 27 pp.
- WATLING, L. 1979. Zoogeographic affinities of northeastern North American gammaridean Amphipoda. *Bull. Biol. Soc. Wash. (1979)* **3**: 256-282.
- WIGLEY, R. L., R. B. THEROUX, AND H. E. MURRAY. 1975. Deep-sea red crab, *Geryon quinquidens*, survey off Northeastern United States. *Marine Fish. Rev.* **37(8)**: 22 pp.
- ZINN, D. J. 1937. The growth and development of starfish in Narragansett Bay in relation to temperature and food supply. *M. S. Thesis, Univ. Rhode Island*, 38 pp.